ISSN 0753-4973

ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY





September 1991 Volume 9, N° 3



International Society for the Study and Conservation of Amphibians
(International Society of Batrachology)

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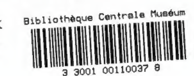
INTERNATIONAL JOURNAL OF BATRACHOLOGY

September 1991 **Volume 9, N° 3**

Predator-prey relationship between giant water bugs (*Belostoma oxyurum*) and larval anurans (*Bufo arenarum*)

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The relationship between an invertebrate predator (*Belostoma oxyurum*, Hemiptera, Belostomatidae) and its prey (*Bufo arenarum*, Anura, Bufonidae) was analyzed experimentally. Both species were collected in a small semi-permanent pond near Buenos Aires, Argentina. In replicated trials, tadpoles of three developmental stages were held at five densities and offered to individual predators of three developmental stages representing several predator sizes. We analyzed the effect of prey stage and size, predator stage, and prey density on the proportion of eaten tadpoles. Predation rate (individuals consumed / predator.time) was higher on smaller preys, except at the highest prey density, independent of predator size and stage. At large prey size, the predation rate was higher for adult water bugs than it was for immature water bugs. The predation rate was low at the highest prey density tested (32 individuals), particularly when the smallest preys were offered to one adult giant water bug.

Larval amphibian population structure has been regarded to be greatly influenced by intraspecific competition, particularly where density-dependent differential growth rate causes unequal competitive abilities among amphibian larvae (SMITH-GILL & GILL, 1978; WILBUR, 1980). However, predation can be more important than intraspecific competition in regulating anuran populations and communities (CRUMP, 1984). Furthermore, tadpole differential growth rates also affect predatory impact upon them, especially if predators display size preferences among their preys (BRODIE & FORMANOWICZ, 1983; SEMLITSCH & GIBBONS, 1988).

It is frequently observed that anurans colonize ephemeral as well as semi-permanent lentic environments, which usually lack efficient piscine predators on their larvae (e.g., GRUBB, 1972). However, improvement in survival associated with this behavior could be counterbalanced by the mortality inflicted by the abundant predaceous insects commonly detected in this kind of limnotope (BROCKELMAN, 1969; CALDWELL et al., 1980; CALEF, 1973; CRONIN & TRAVIS, 1986; CRUMP, 1984; FORMANOWICZ & BRODIE, 1982; HEYER et al., 1975; KEHR & BASSO, in press; SMITH, 1983).

In contrast to piscine predation, the success of predatory insects is strongly limited by the size of potential preys. Beyond a certain maximum size tadpoles may become invulnerable to insect predation. Therefore, an increase in the prey growth rate can be a selective advantage (TRAVIS, 1983; TRAVIS et al., 1985). In particular, as tadpoles become larger, they become invulnerable to predatory attacks by odonate naiads (BRODIE & FORMANOWICZ, 1983; HEYER & MUEDEKING, 1976; HEYER et al., 1975; PRITCHARD, 1965) and adult *Belostoma* sp. (BRODIE & FORMANOWICZ, 1983). *Aeschna* naiads, however, are able to capture and kill all stages of *Hyla pseudopuma* offered (CRUMP, 1984).

The size limitation of insects that prey on larval amphibians has been a matter of controversy during the last decade. CALDWELL et al. (1980), for example, suggested that dragonfly naiads *Anax junius* are not size limited, since they can hold on to large struggling prey of *Hyla gratiosa*. Conversely, BRODIE & FORMANOWICZ (1983) stated that *Belostoma* sp. and *A. junius* of all tested sizes killed and consumed more small tadpoles than large ones, whereas *Lethocerus* sp. exhibited no preference for prey size (30-38, GOSNER, 1960).

Small tadpoles may be able to avoid insect attacks by being unpalatable. *Bufo americanus*, for example, has been regarded as unpalatable, not only to sucking (*Belostoma* sp.) and chewing (*A. junius*) invertebrate predators, but also to vertebrate predators (BRODIE & FORMANOWICZ, 1987). Previously, WASSERSUG (1973) postulated that unpalatability was not an effective strategy for amphibians to reduce predation by invertebrate predators which suck body fluids.

Another prey benefit can be attained by aggregation (BRODIE & FORMANOWICZ, 1987). The several proposed mechanisms include the "confusion" of predator to select individual prey from an aggregation (MILINSKI, 1979; TREHERNE & FOSTER, 1981).

Some of the above ideas were tested experimentally with a predator-prey system composed of giant water bugs and larval anurans. Giant water bugs are conspicuous insects that inhabit lentic environments where they are important predators upon anuran populations. A predator (*Belostoma oxyurum*, Hemiptera, Belostomatidae) and a prey (*Bufo arenarum*, Anura, Bufonidae) species were selected to evaluate the following factors : (1) the influence of the size of the predator and prey on their interactions ; (2) the effects of prey density on predation rate ; and (3) the existence or non-existence of a prey size threshold for water bug predation.

METHODS

THE TEST SPECIES

Geographically, *B. oxyurum* is one of the more restricted species among the South American belostomatids. It occurs in the southern portion of the "Mesopotamia" and along most of the oriental border of the Pampasic Dominion (RINGUELET, 1961), in Argentina.

In the area where the tested *B. oxyurum* specimens were captured, giant water bugs are multivoltine. Only fifth instar nymphs and adults overwinter. First instar nymphs hatch

from overwintering incubant males by the beginning of spring, and they reach the adult stage in about fifty days (DOMIZI et al., 1978). Females of *Belostoma*, as well as other genera of the Belostomatinae, glue their eggs on the dorsum of males, who carry and care for them until they hatch (MENKE, 1979).

All five nymphal instars and adults of *B. oxyurum*, like other species of belostomatids, are efficient predators. Their "sit-and-wait" predatory tactic (SCHOENER, 1969) is non-selective, i.e. the predator usually lies in ambush for occasional prey. The ability of giant water bugs to make successful attacks is due to their strength, tenacity, and the paralyzing effect of the toxin injected by these sucking predators to subdue prey (PICADO, 1937; DE CARLO, 1959; MENKE, 1979).

Bufo arenarum is widespread in Argentina, occurring from northern Jujuy Province to the Chubut river, near the Patagonian Coast, and in Southern Brazil, Uruguay and Bolivia. Its reproduction is potentially continuous, since spawning and egg laying extend through most of the year. From August to April, metallic-sounding choruses of this toad can be heard in natural or artificial ponds or lagoons after occasional rainfalls. The small, black-colored eggs are laid in large, gelatinous strings, placed at random on the bottom. Average clutches of 4000-5000 eggs are usual for a seasonal spawning of a single mature female. During the winter, *B. arenarum* is rarely found, since it is hidden in natural refuges or underground (CEI, 1980).

Both tested species, *B. oxyurum* and *B. arenarum*, display synchronous sexual cycles in the collecting site, where mating and egg laying take place from August to April.

STUDY SITE AND COLLECTING PROCEDURE

The predator and the prey were collected in a small semi-permanent pond located at Los Talas, District of Berisso, Buenos Aires, Argentina. Only the fourth and fifth instar and adult stages of the water bugs were used in this study. Each stage of development was held separately in a plastic bag and starved after capture for 48 h prior to the start of a trial. Anuran tadpoles were collected at the same time but kept separately in plastic containers. Tadpoles not eaten or injured were either used again (only in three different trials) or released.

EXPERIMENTAL DESIGN

Three groups of tadpoles in different stages were used : (1) stages 26-29 ; (2) stages 31-35 ; and (3) stages 38-40 (GOSNER, 1960). Tadpoles of each stage of development, at different densities (2, 4, 8, 16 and 32 individuals), were offered to one predator of each stage of development tested (IV, V and adult stage) in 15 × 15 cm all-glass aquaria containing 2 l of previously dechlorinated water. Three replicates for each 24 h trial were performed, for each of the nine trials (three for each tadpole stage and three for each predator stage) by tadpole density tested (five densities). The various tadpole stages, tadpole densities and predator stages were provided in separate trials. As each predator was utilized only once, 27 predator individuals were needed for each tadpole density.

Hence, a total of 135 predator individuals were used for all experiments. Adult predators of each sex were randomly assigned to each treatment (sex identification is only possible for adult stages). The predators were weighed in advance to ± 1 mg precision. Remaining tadpoles were counted at the end of each experiment. Temperatures ranged from 20° to 24°C. A similar experimental design with two replicates for the smaller prey sizes tested (stages 26-29) was performed with mature water bugs to evaluate effects of predator incubating activity. To examine differences in predation due to the sex of adult water bugs, individual male and female water bugs were offered small tadpoles at two densities (4 and 16 tadpoles) in separate trials (two replicates per each sex). All collections and experiments in this study took place between August and December, 1987.

Analytical procedure

Data were recorded as number of tadpoles eaten for each treatment. Several statistical tests were used to analyze the data. For tests on the proportions of tadpoles eaten (# eaten / # offered), arc-sine transformations were performed before analysis.

A Chi-square test with "Yates correction for continuity" was used to assess the effects of predator, sex, and reproductive condition of males (encumbered vs. unencumbered) on the number of tadpoles eaten by adult water bugs. The Kruskal-Wallis test was used to determine differential predation rates, with respect to: (a) tadpole stage; (b) tadpole density; and (c) predator stage. In addition, a non-parametric Tukey-type multiple comparisons test (Zar, 1984) was applied for each of these three relations. Since comparisons were analyzed by "mean ranks" and not by "sum ranks", the S.E. (standard error) was obtained, as proposed by Miller (1966). The significance level of both tests was $\alpha = 0.05$.

Preliminary tests were performed to analyze interactions between variables and to examine the homogeneity of the group variances, for subsequent application of a Multivariate Analysis of Variance (MANOVA) on the proportions of tadpoles eaten. All treatments and interactions were included in the MANOVA. Some may object to the use of this test, due to the non-normal distribution of data, particularly at the lower prey densities (2 and 4 tadpoles). Therefore, we also performed the non-parametric tests described above. The significance level for the MANOVA was arbitrarily selected as $\alpha = 0.001$.

Results

Table I summarizes the data for the mean number of tadpoles eaten per predator, for each treatment shown (3 replicates / treatment). Although not statistically significant, differences were observed for the numbers of tadpoles eaten by the two sexes and by encumbered vs. unencumbered males. The following results were obtained for separate Chi-square tests (in each, $P > 0.05$, d.f. = 1) : (1) for encumbered vs. unencumbered males, at 2, 4, 8, 16 and 32 tadpole densities respectively, $\chi^2 = 3.21$, $\chi^2 = 0.01$, $\chi^2 = 0.81$, $\chi^2 = 0.59$ and $\chi^2 = 0.15$; and (2) for male vs. female water bugs, $\chi^2 = 0.01$ (4 tadpoles) and $\chi^2 = 0.88$ (16 tadpoles).

Table I. — Prey size and density preferences of giant water bugs, nymph and adult *Belostoma oxyurum*, for *Bufo arenarum* tadpoles.

Predators			Tadpoles [1] eaten / 24 h			
				Stage (GOSNER, 1960)		
				26-29	31-35	38-40
Stage of predator [2]	Weight (mg) $\bar{x} \pm$ S.D.	n	n each offered	Weight (mg) $\bar{x} \pm$ S.E. 0.019 ± 0.002	Weight (mg) $\bar{x} \pm$ S.E. 0.088 ± 0.002	Weight (mg) $\bar{x} \pm$ S.E. 0.178 ± 0.020
IV	0.034 ± 0.004	1	2	2.00 ± 0	0.00 ± 0	0.00 ± 0
		1	4	4.00 ± 0	0.00 ± 0	0.00 ± 0
		1	8	7.60 ± 0.37	0.00 ± 0	0.00 ± 0
		1	16	3.00 ± 1.60	3.00 ± 0	0.00 ± 0
		1	32	13.30 ± 4.50	1.33 ± 0.47	1.00 ± 0
V	0.104 ± 0.010	1	2	2.00 ± 0	0.00 ± 0	1.00 ± 0
		1	4	3.70 ± 0.27	0.00 ± 0	1.00 ± 0
		1	8	4.20 ± 1.30	2.00 ± 0	2.00 ± 0.81
		1	16	8.00 ± 2.12	2.00 ± 0	2.00 ± 0.75
		1	32	4.10 ± 1.50	4.00 ± 0.81	2.00 ± 0.81
Adults unencumbered	0.152 ± 0.034	1	2	2.00 ± 0	2.00 ± 0	2.00 ± 0
		1	4	3.00 ± 0.73	4.00 ± 0	3.50 ± 0.47
		1	8	6.60 ± 1.24	3.30 ± 1.80	3.00 ± 0.80
		1	16	10.33 ± 0.47	7.00 ± 0.81	2.50 ± 1.20
		1	32	5.66 ± 2.50	10.00 ± 3.10	3.00 ± 0.82

1. Each trial lasted 24 h and was replicated three times.
2. Each predator was used for only one trial.

The proportions of preys eaten were significantly different for the three tadpole stages tested (Kruskal-Wallis test: $H = 30.83$, $P < 0.01$) (Table II). The analysis performed to determine the levels where differences occurred (non-parametric, Tukey-type multiple comparisons test), reflected two homogeneous groups (1: tadpole stages 26-29; 2: tadpole stages 31-35 and 38-40) (Table II). By examining Table I, it is evident that the group of smaller tadpoles was more vulnerable to predation.

The influence of tadpole densities on predation was evident (Kruskal-Wallis test: $H = 11.26$, $P < 0.05$) (Table II). However, pairwise significant differences were detected only between the extreme densities tested (2 vs. 32 tadpoles), with proportionately more of the tadpoles at lower densities being eaten. Compared to later predator stages, fourth instar water bugs ate a larger proportion of the small tadpoles at high densities. At the highest prey densities, adult water bugs ate proportionately more of the medium-sized prey (31-35) (Table I).

A significant heterogeneity was estimated in two of the groups (tadpole stage and tadpole density). However, the MANOVA test (Table III) revealed trends that were similar

Table II. – Analysis of arc-sine transformation of proportion eaten (# tadpoles eaten / # tadpoles offered), for two non-parametric tests for each of three levels tested: tadpole stages; tadpole densities; and predator stages.

Level tested	Sample size	Mean rank	Non-parametric [1] multiple comparisons (homogeneous groups)	
Bufo stage				
1 (26-29)	45	94.1444	*	
2 (31-35)	45	55.4889		*
3 (38-40)	45	54.3667		*
Kruskal-Wallis test : H = 30.8325; P < 0.01.				
Bufo density				
1 (2 tadpoles)	27	81.5556	*	
2 (4 tadpoles)	27	77.6481	*	*
3 (8 tadpoles)	27	69.3889	*	*
4 (16 tadpoles)	27	60.3704	*	*
5 (32 tadpoles)	27	51.0370		*
Kruskal-Wallis test: H = 11.2650; P < 0.05.				
Belostoma stage				
3 (adults)	45	90.6444	*	
2 (stage V)	45	64.5556		*
1 (stage IV)	45	48.8000		*
Kruskal-Wallis test : H = 26.8459; P < 0.01.				

1. Non-parametric, Tukey-type multiple comparisons test.

to those obtained with the non-parametric tests described above. The MANOVA analysis showed highly significant differences for all treatments (predator stage, tadpole density and tadpole stage), as well as for all interactions.

Discussion

Smaller tadpoles were more vulnerable to predation than larger ones for all of the tested stages of water bugs in these studies. Nevertheless, adult predatory rate declined as the newly-hatched preys were offered at the highest experimental density (32 individuals). We rejected the explanation that a large adult giant water bug is unable to subdue a much smaller prey, because, at low experimental densities, predation rate on the smallest prey was high, regardless of predator size. The lack of efficiency of adult giant water bugs to predate on tiny tadpoles could be due to the "confusion" in selecting individual prey from an aggregation (Milinski, 1979; Treherne & Foster, 1981; Brodie & Formanowicz, 1987; Kehr, in press a). A benefit to clumped tadpoles might be a reduction of individual

Table III. — Analysis of arc-sine transformation of proportion eaten (# tadpoles eaten / # tadpoles offered), using a MANOVA test on the three levels tested: tadpole stages (tadstage); tadpole densities (taddens) and predator stages (prestage).

Source of variation	S.S.	D.F.	M.S.	F	Sign. of F
Within cells	4.72	90	0.05		
Constant	60.02	1	60.02	1144.76	.0001
Tadstage	10.85	2	5.43	103.49	.0001
Taddens	6.46	4	1.61	30.80	.0001
Prestage	6.81	2	3.41	64.98	.0001
Tadstage by taddens	3.32	8	0.41	7.91	.0001
Tadstage by prestage	4.74	4	1.19	22.61	.0001
Prestage by taddens	3.08	8	0.39	7.35	.0001

risk to predation. A member of the group, while hidden behind other individuals, has just one chance in many of being caught by one predator (ALCOCK, 1979). Newly-hatched *B. arenarum* usually aggregate in nature (KEHR, in press b).

The overall water bug predatory trend showed a positive preference for smaller prey, particularly by fourth and fifth instar predators (Table I). Probably, immature water bugs are more susceptible to danger of injury to the prey-capturing apparatus (BRODIE & FORMANOWICZ, 1983), and they also may require longer handling times for subduing large prey than adult giant water bugs. The stronger predatory structures of *B. oxyurum* adults certainly make them less exposed to injury. Nevertheless, the highest predation rate of adult predators was observed on tadpoles of stages 26-29 and 31-35, being lower on larger individuals.

A reduction of predatory efficiency has been suggested for encumbered males of the giant water bug *Abedus herberti* from Central Arizona (SMITH, 1976 a). This reduction is partially attributed to the limitation imposed by the higher weight of the incubant males. In addition, it has been pointed out that in several groups of giant water bugs a brooding male spends many hours resting near the surface to aerate fertilized eggs. During this time it is assumed that an encumbered male cannot feed efficiently (SMITH, 1976 b; ALCOCK, 1979). Data obtained during this study show that *B. oxyurum* can double its weight when heavily encumbered by eggs. Although male water bug incubating activity could reduce predatory efficiency, differences between encumbered and unencumbered *B. oxyurum* were not significant. This observation is logical, because tadpole capture by ambush predators could be facilitated more by the motion of the tadpole than by active chasing by the predator (MENKE, 1979).

Unpalatability to vertebrate predators, as well as to both sucking (*Belostoma* sp.) and chewing (*Anax junius*) insect predators, has been pointed out for newly-hatched *Bufo americanus* tadpoles (BRODIE & FORMANOWICZ, 1987). Chemical cues to deter predation, associated with schooling, are assumed to be competitively advantageous for *B. americanus* tadpoles (WALDMAN, 1982; WALDMAN & ADLER, 1979; BRODIE & FORMANOWICZ, 1987). Our experiments support the inference that newly-hatched *B. arenarum* tadpoles are palatable to giant water bugs.

WASSERSUG (1973) and WALDMAN & ADLER (1979) postulated the evolution of aggregations in the larvae of unpalatable amphibians. However, although unpalatability may be a precursor of the evolution of aggregations, aggregations should not be viewed as a precursor of the evolution of unpalability (BRODIE & FORMANOWICZ, 1987). Our results are compatible with this hypothesis. Aggregation in *B. arenarum* could play a similar role to unpalatability in *B. americanus*. This might mean that a behavioral mechanism would substitute for a physiological one in order to lessen predatory impact upon newly-hatched tadpoles.

ACKNOWLEDGEMENTS

We are grateful to Dr. Richard J. WASSERSUG and two anonymous reviewers for the critical review of the manuscript.

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Images d'Amphibiens camerounais. IV. Les constructeurs de nids

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In Cameroon, the Anurans of three genera (*Afrixalus, Opisthothylax* and *Chiromantis*) build "nests" above the water. In the three cases, both parents cooperate in the construction of the nest. The latter is here particularly described, and illustrated with photos, in *Afrixalus* and *Opisthothylax*. The function of the nests seems to be different according to the genus.

La chambre de ponte des *Hemisus*, évoquée dans un précédent article (Amiet, 1991), peut être considérée comme un nid. Le même terme pourrait s'appliquer aussi aux cavités creusées par certains *Leptopelis* ou *Arthroleptis* pour abriter leurs œufs

Les nids montrés par les photos des figures 1 à 6 sont d'un type très différent. Ils sont en effet construits au-dessus de l'eau grâce à une collaboration active des deux parents et intègrent des éléments de la végétation environnante.

Ce mode de nidification est pratiqué au Cameroun par trois genres d'Anoures: *Afrixalus, Opisthothylax* et *Chiromantis*

Le nid des *Afrixalus*

Le genre *Afrixalus* regroupe des petites rainettes d'aspect assez proche de celui des *Hyperolius*. On y reconnaît environ 25 espèces. Quelques-unes sont sylvicoles mais la plupart vivent dans les formations secondaires en zone forestière ou dans des savanes plus ou moins sèches.

Il semble que les premières descriptions de nids d'*Afrixalus* aient été faites par Wager (1965), à qui l'on doit de fines observations sur les Anoures d'Afrique australe. Peu après, Schiøtz (1967) a donné des informations sur la nidification de plusieurs espèces d'Afrique de l'Ouest, dont *A. weidholzi*, espèce existant aussi au Cameroun.

La photo de la figure 1 montre dans quelle position acrobatique un couple d'une espèce camerounaise, *A. paradorsalis*, construit son nid Celui-ci est toujours constitué par l'extrémité d'une feuille (souvent de Zingibéracée ou de Marantacée) qui est repliée *longitudinalement*, suivant la nervure principale. Mieux qu'une longue description, la photo

permet de comprendre comment ce résultat est obtenu par le mâle et la femelle en amplexus. Les deux partenaires doivent faire preuve d'une remarquable coordination gestuelle pour rapprocher les bords du limbe et les maintenir jusqu'au moment où la substance visqueuse enrobant les œufs leur permettra de les faire adhérer l'un à l'autre. Terminé, le nid passe totalement inaperçu dans la végétation. En général, il est placé de 1 à 2 m au-dessus de l'eau.

Tous les *Afrixalus* ne procèdent pas de la même façon. D'après SCHIØTZ (1967), une petite espèce de savane, *A. weidholzi*, utilise une feuille de Graminée qu'elle replie transversalement ("transversally folded grass leaves"). Le nid d'*A. nigeriensis*, espèce d'Afrique occidentale, peut comprendre "one or few leaves folded and glued round a rather small mass of eggs".

Un *Afrixalus* strictement sylvicole, *A. laevis*, pose un problème évolutif intéressant car il ne construit pas de nid: comme on peut le constater par la figure 3, les œufs, au nombre d'une demie douzaine au maximum et de teinte vert pâle, sont déposés sur ou sous une feuille sans aucune protection et parfois même bien en évidence. Les pontes surplombent de petits cours d'eau, où se développent les têtards. *A. laevis* représente-t-il une "espèce primitive" qui aurait conservé le mode ancestral d'oviposition ou, au contraire, a-t-il abandonné secondairement la méthode de nidification de ses congénères ? Je penche pour la seconde hypothèse, étayée par le fait que le têtard d'*A. laevis* est allé plus loin que celui des autres *Afrixalus* dans la réduction de la formule dentaire puisqu'il n'a plus du tout de denticules cornés, alors qu'il en reste une rangée, sous le bec, chez les autres espèces. De même, l'habitat du têtard en eau courante s'oppose à celui des autres *Afrixalus*, tous inféodés aux eaux stagnantes, et peut être conçu comme une "percée évolutive" réalisée par cette espèce[1].

LE NID D'*OPISTHOTHYLAX IMMACULATUS* (BOULENGER, 1903)

Cette rainette sylvicole, dont l'aire de distribution ne dépasse guère les limites du Cameroun, est aisément reconnaissable à sa pigmentation dorsale jaune, orange ou brun-roux uniforme à l'exception de deux petites macules noires occipitales. Elle se distingue de tous les autres Hyperoliidae par le fait que sa ponte est incluse dans une sorte de mucus battu comme chez les Rhacophoridae.

La masse spumeuse, peu volumineuse, et les œufs (une dizaine au plus, de 4,6 mm de diamètre) se trouvent à l'intérieur d'une feuille repliée *transversalement*. L'ensemble constitue un nid très discret, placé au-dessus d'un petit cours d'eau (AMIET, 1974).

Postérieurement à la description du nid dans le travail cité, j'ai eu la chance de pouvoir observer et photographier sinon toute son élaboration, du moins la phase finale, illustrée par la figure 5.

1 La formule dentaire et l'habitat du têtard d'*A. lacteus*, une espèce orophile, sont semblables à ceux d'*A. laevis* mais je n'en connais pas la ponte : il serait intéressant de savoir si le mode d'oviposition confirme les affinités entre ces deux espèces. Remarquons d'autre part que le comportement de ponte si élaboré des *Afrixalus* ne plaide pas pour leur regroupement avec les *Kassina* dans une même tribu ou sous-famille, statut proposé par LAURENT (1982, 1986) mais récusé par DREWES (1984).

Les premières phases peuvent cependant être facilement reconstituées. Au terme d'une "promenade nuptiale" du couple en amplexus (fig. 4), une feuille convenable est trouvée: elle doit pendre plus ou moins verticalement au-dessus de l'eau. Les ovules sont émis et fécondés sur le limbe, la face n'important pas (sauf, peut-être, si la face supérieure est trop envahie d'épiphylles). La ponte est accompagnée d'un liquide visqueux apparemment sécrété par la partie distale, très élargie, des oviductes (AMIET, 1974).

Le mâle, après avoir fécondé les œufs, passe de la position d'amplexus axillaire à la position lombaire et, à l'aide de ses pieds, saisit l'extrémité de la feuille *par l'autre face*, la replie et la glisse entre son ventre et la région postéro-dorsale de la femelle.

C'est cette dernière qui, seule, bat le mucus en agitant ses pattes dans le repli de la feuille: la photo de la figure 5 est prise à ce stade d'élaboration du nid Elle montre bien la position assez extraordinaire des pieds du mâle pendant cette phase et permet de constater qu'il y a une certaine opposabilité des deux orteils les plus internes, facilitant la "mise en pli" de la feuille.

Quand le mucus battu a atteint une consistance suffisante pour que la pliure persiste, le mâle s'éloigne après que la femelle se soit avancée un peu sur la feuille où, visiblement fatiguée, elle s'accorde un moment de repos.

J'ai émis l'hypothèse (AMIET, 1974) que le comportement nidificateur d'*Opisthothylax* pouvait être dérivé de celui des *Afrixalus*, mais il est possible aussi qu'il s'agisse d'une simple convergence. Une analyse détaillée des séquences gestuelles lors de la construction du nid chez les diverses espèces d'*Afrixalus* et chez *Opisthothylax* permettrait peut-être de trancher entre ces deux hypothèses.

LE NID DE *CHIROMANTIS RUFESCENS* (GÜNTHER, 1868)

Les Rhacophoridae, nombreux en Asie et à Madagascar, ne sont représentés en Afrique que par un seul genre, *Chiromantis*, comprenant deux espèces savanicoles en Afrique orientale et australe et une espèce répandue dans la zone forestière mais plutôt parasylvicole, *C. rufescens*.

Au Cameroun, cette espèce a été bien étudiée par MONAYONG AKO'O (1978). Le nid, comme chez les autres espèces du genre, est constitué par une volumineuse masse d'écume, d'environ 12-15 cm de plus grande dimension, dont la surface durcit plus ou moins en lui donnant l'aspect d'une meringue. Il contient une centaine d'œufs mesurant environ 2 mm de diamètre.

Le mâle (ou les mâles, car il est fréquent que plusieurs s'accouplent avec la même femelle) coopère à l'élaboration du nid: les partenaires, accouplés, battent de leurs pattes postérieures une substance glaireuse produite par la femelle et la "montent en neige". Le nid peut ou non incorporer des feuilles de la plante servant de support et n'est d'ailleurs pas forcément déposé sur un support végétal: un rocher surplombant l'eau, les parois des profondes ornières creusées par les engins forestiers, sont souvent utilisés. De même, la hauteur du nid au-dessus de l'eau est très variable, de quelques centimètres à 2 ou 3 m.



1



2



3

Fig 1 Couple d'*Afrixalus paradorsalis* Perret, 1960 en train de pondre dans une feuille repliée Kala, 10-III-76.

Fig 2 Un nid d'*Afrixalus paradorsalis* ouvert, montrant les jeunes larves encore incolores. Kala, IV 81

Fig 3. Ponte d'*Afrixalus laevis* (Ahl, 1930). Cette ponte n'est pas nécessairement placée à l'extrémité d'une feuille comme sur la photo. Kala, 4-XI-74.

4

5



6

Fig. 4 – Couple d'*Opisthothylax immaculatus* (Boulenger, 1903) en "promenade nuptiale". Les gros ovules sont visibles par transparence sous la peau du flanc droit de la femelle. Nkoladzap, 12-III-76.

Fig. 5 – Fin de la construction du nid chez *Opisthothylax immaculatus*. Pendant que le mâle tient la feuille repliée, la femelle bat le mucus dans lequel sont inclus les œufs. Nkoladzap, 12-III-76.

Fig. 6. Nid d'écume de *Chiromantis rufescens* (Günther, 1868) adhérant à une feuille. Comme on peut le constater, ce nid est très apparent. Yaoundé, XI-73.

Le rôle des nids

Tout comme pour la garde des œufs, on peut s'interroger sur le rôle des nids qui viennent d'être décrits.

Deux fonctions possibles viennent à l'esprit : (1) dissimuler la ponte à d'éventuels prédateurs; (2) la protéger contre la dessiccation et/ou l'action directe des rayons solaires

Il est certain que les nids d'*Afrixalus* et d'*Opisthothylax* sont, dans la nature, très difficiles à détecter (du moins pour l'homme, car il n'est pas sûr qu'ils puissent échapper à la vue d'un oiseau!) et peuvent de ce fait assurer aux œufs une protection contre les prédateurs. Encore faudrait-il que ceux-ci existent dans la faune camerounaise: comme je l'ai déjà fait remarquer (Amiet, 1991), il n'a pas été possible jusqu'ici d'avoir la preuve qu'un quelconque prédateur (à l'exception de celui dont il sera question ci-après) puisse s'attaquer à des pontes d'Anoures dans le territoire étudié. Le fait qu'*A. laevis* ait apparemment "renoncé" à la construction d'un nid et laisse ses œufs en évidence comme nombre d'autres rainettes à ponte suspendue montre d'ailleurs que, au stade œuf, la prédation ne doit pas constituer une contrainte évolutive efficace.

Le nid de *Chiromantis rufescens*, contrairement à celui des *Afrixalus* et *Opisthothylax*, est très apparent en raison de sa grande taille et de sa teinte, caractères qui seraient difficilement concevables si les œufs étaient en butte à l'action des prédateurs. Pourtant, Brosset (1976) a montré comment, au Gabon, les nids de *C. rufescens* sont souvent mis à sac par un petit oiseau, *Nigrita bicolor*, qui mange les œufs ou les jeunes têtards. Au Cameroun, j'ai pu observer de telles scènes de pillage mais elles m'ont paru tout à fait exceptionnelles (*N. bicolor* "signe" ses déprédations en projetant de tous côtés des éclaboussures d'écume). Il est très possible que ce comportement corresponde à une habitude alimentaire acquise depuis peu (à rapprocher du cas des mésanges ayant appris à décapsuler les bouteilles de lait) et qui ne s'est pas encore généralisée. Si cela se produisait, l'avenir de *C. rufescens* dans les régions peuplées par *N. bicolor* pourrait être sérieusement compromis...

Si le nid ne paraît pas destiné à protéger les œufs contre les prédateurs, qu'en est-il d'une protection contre la dessiccation ou l'action du soleil?

Pour les espèces sylvicoles ou pour les espèces de brousse secondaire dense en zone forestière, celle-ci ne paraît pas nécessaire, compte tenu de l'humidité atmosphérique presque constamment élevée et de l'effet d'écran joué par la végétation. En revanche, pour les Anoures qui se reproduisent en milieu très ouvert, en particulier les savanes sèches, le nid doit assurer une réelle protection contre la sécheresse et l'insolation. Le cas de *C. rufescens*, qui peuple la zone forestière et produit un nid particulièrement volumineux, n'est contradictoire qu'en apparence, d'abord parce que cette espèce n'est pas franchement sylvicole mais vit plutôt dans des formations dégradées paraforestières, et ensuite parce qu'elle fait partie d'un genre plutôt savanicole si l'on en juge par la distribution des autres espèces. Les Anoures de savane ne déposent généralement pas leurs œufs au-dessus de l'eau, ou sinon à faible hauteur, et il est probable que sans la protection apportée par la masse d'écume du nid, les pontes aériennes des *Chiromantis* savanicoles seraient exposées à un prompt déssèchement [2].

2. Il faut rappeler aussi que dans la famille des Rhacophoridae, dont fait partie le genre *Chiromantis*, la production de nids d'écume est pratiquée par la majorité des espèces

En ce qui concerne les *Afrixalus* savanicoles, l'argumentation précédente se trouve cependant affaiblie par quelques espèces d'Afrique australe qui construisent leur nid *sous* l'eau! Ce comportement a été observé par WAGER, qui en donne une photo (WAGER, 1965). On peut imaginer que le nid, en changeant de milieu, change aussi de fonction et qu'il assure alors une protection des œufs contre les prédateurs, probablement plus nombreux en milieu aquatique qu'en milieu aérien.

Le cas du nid d'*Opisthothylax* me paraît devoir être dissocié des précédents. Chez cette rainette en effet les œufs sont riches en vitellus (4,6 mm de diamètre!) et les larves ne sortent du nid que 2 à 3 semaines après la ponte, déjà munies de bourgeons de pattes postérieures (AMIET, 1974). Le jeune têtard est alors plus apte à affronter les risques de la vie libre, tels que les prédateurs, mais aussi le courant puisque la suite du développement se fait dans de petites rivières. En construisant son nid, le couple d'*Opisthothylax* travaille au moins autant pour les têtards que pour les œufs...

RÉSUMÉ

Au Cameroun, les Anoures de trois genres (*Afrixalus, Opisthothylax* et *Chiromantis*) construisent des "nids" situés au-dessus de l'eau. Dans les trois cas, les parents coopèrent à l'élaboration du nid. Celle-ci est particulièrement décrite, et illustrée de photos, chez *Afrixalus* et *Opisthothylax*. La fonction des nids paraît différer suivant les genres considérés

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Variation in size and fecundity between neighbouring populations in the common frog, *Rana temporaria*

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Differences in body size were detected among neighbouring populations of common frogs (*Rana temporaria*) in Jurassian Bresse (Eastern France). Variation in fecundity and egg size was positively correlated with body size. Frogs using one wooded area were smaller than those elsewhere. Small body size might result from a slower growth rate or from earlier sexual maturation. Demographic parameters of these French populations differed from those of other European populations, but no correlation between demographic parameters and latitude or altitude were detected.

INTRODUCTION

Variation in demographic parameters on a geographic scale (cline or isolated populations) has been the subject of considerable attention in anurans (MARTOF & HUMPHRIES, 1959; PETTUS & ANGLETON, 1965; KOSLOWSKA, 1971; NEVO, 1972; KOSKELA & PASANEN, 1975, BERVEN, 1982, 1988; READING, 1988, 1990), but variation on a smaller scale has received little study Isolation of populations may lead to genetic adaptation to local environmental conditions (BERVEN, 1982, 1988); when genetic exchange between local populations becomes frequent, variation reflects the influence of epigenic factors on phenotypes Among such mechanisms of plasticity, differences in growth rate can determine variation in adult size, age at maturity, fecundity and egg size (BERVEN & GILL, 1983; STEARNS & KOELLA, 1986).

Estimating the level of isolation between neighbouring populations is difficult; site fidelity can play a discrete isolating role (OLDHAM, 1963; HAAPANEN, 1970). I studied neighbouring demes of *Rana temporaria* (the common frog) that had been subjected to numerous transfers of tadpoles over a period of twenty years. In the Jurassian Bresse

region of France, common frogs are heavily harvested from certain ponds by professional fish-farmers. This practice is authorized on condition that the frogs be allowed to spawn before being killed; eggs or tadpoles are taken back to the ponds without taking into account the original site of their parents. Such a mix has been occurring for 15 years, and one may assume the local populations to be genetically homogeneous. This paper demonstrates variation of body size among these demes and defines the relationship of adult size with fecundity and egg size Characteristics of Jurassian Bresse populations are compared with those from other regions of Europe.

Materials and methods

The Jurassian Bresse region (north of Lons-le-Saulnier, Jura Department) varies between 200 and 250 m in altitude. The main ecosystems are forests (*Quercus*, *Fraxinus* and *Carpinus*), agrosystems alternating between pastures and crop, and shallow ponds devoted to carp culture. These ponds vary in area from 2 to 20 ha and in depth to a maximum 3 m at the draining point; average depth is approximately 0.7 m. Ponds are drained every winter to fish the carp and are then filled with water from small brooks or rain. Most ponds are surrounded by forest. The common frog is abundant, several thousands individuals breed in certain ponds. In each pond, frogs gather in one or several spawning sites, where their eggs are clumped. In 1986 and 1987, frogs were sampled in ponds A (Servotte, 19.7 ha) and B (Thévenon, 3.5 ha) during the breeding season (fig. 1). The distance between these ponds is about 9 km and their altitude is similar (220 m). In 1987, populations of three other ponds were sampled (C: Roche, 2.5 ha; D: Chardennet, 6.6 ha; E: Neuf, 3 ha). All five ponds are situated along a 20 km North-South transect.

Frogs were caught around spawning areas in traps installed by pisciculturists, weighed using Pesola letter-scales (precision 0.1 g), and measured from snout to urostyle with vernier calipers. Only gravid females were weighed. Females from ponds A and B were dissected to obtain clutch weights and egg counts (site A: n = 27; site B n = 22). Because oocytes are coated with a sticky gelatinous envelope preventing their being counted easily, it was not possible to estimate egg number, spawn mass, and oocyte mass from the same individual. Dissolving mucins in the envelope involves the use of potassium cyanide (2 hours in a 20 % KCn solution) which may also damage oocyte proteins and modify their mass. I extracted eggs by dissection of the spawn immediately after laying, before egg mass began to increase (it remains stable for 12 hours after spawning; Cummins, 1986). The clutch obtained by dissecting a female provided the wet weight of both oocyte and jelly and the egg extracted after spawning allowed for measurement of wet and dry mass. Correlation and regression analyses of female body size and these different parameters were performed. Clutch wet weights were combined for the two years under study, while egg wet and dry mass data were collected in 1987 only. In 1987, males and females from ponds A and B were paired (n = 22) and isolated in 40 × 40 × 10 cm tanks for spawning. Within 12 hours after egg laying, 30 eggs were extracted from the gelatinous envelope by

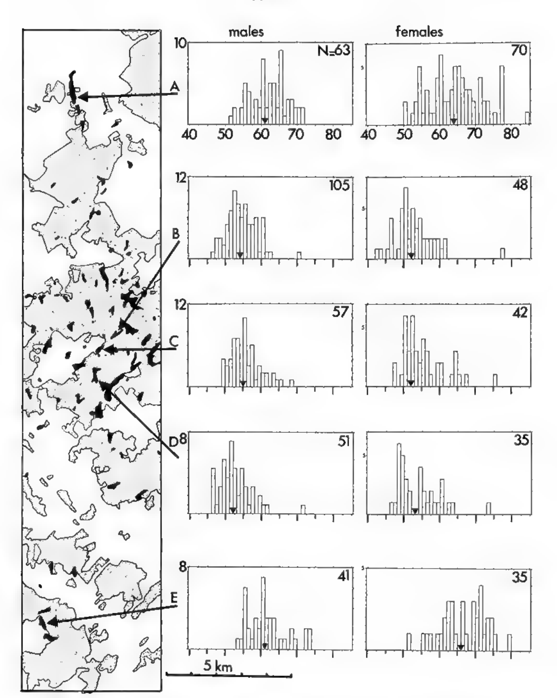


Fig. 1. — Distributions of frog lengths in five ponds along a 20 km long transect. Black patches: ponds. Dotted area: forest. White area: cultures and pastures. On the graphs, the triangles indicate mean values. A: Servotte; B: Thévenon, C: Roche, D: Chardennet; E: Etang Neuf. Demes of small frogs were found at B, C and D; those ponds are grouped in the same forest area, where density of ponds is higher than elsewhere.

dissection, clumped in groups of 10, weighed, and then dried for 48 h at 80°C. This procedure gives a better estimation of egg size than measuring egg diameter, and allows the estimation of reproductive investment (Cummins, 1986).

Results

Body size

Size distributions of males and females were approximately normal. During 1986 and 1987, males and females from site B were, on average, 1 cm smaller and 10 g lighter than those from site A (Table I). Variation from one year to the other was also significative. In order to determine where small size occurred, three other ponds situated approximately along a 20 km transect which includes ponds A and B at the North end (fig. 1) were sampled during the breeding season of 1987 Ponds C and D (Roche and Chardennet) are situated in the same forest as B, while pond E (Etang Neuf de Lombard) is close to another forest area to the South. Length of frogs breeding in ponds B, C and D was significantly smaller than length of frogs breeding in A and E (ANOVA, F test: $P < 0.0001$ for both males and females). Frogs from B, C, and D were significantly smaller than those from A and E in all pair-wise comparisons (Fisher PLSD). Snout-urostyle length did not vary significantly between A and E and snout-urostyle length of frogs from B, C and D are not different from each other. A smaller size was not a characteristic of frogs inhabiting pond B, but was related to that group of demes (B, C, D) inhabiting the forest area (Bois de Champrougier).

Table I. - Comparison of length (mm) and weight (g) of frogs from ponds A and B for two years (t test). Frogs from A are always larger than those from B.

			Site A			Site B			P
			n	$\bar{x}$	σ	n	$\bar{x}$	σ	(t test)
Males	1986	length (mm)	87	66.1	6.4	79	56.4	5.3	< 0.0001
		weight (g)		26.5	7.9		16.0	5.3	< 0.0001
	1987	length (mm)	63	61.7	5.1	79	54.6	4.1	< 0.0001
		weight (g)		26.0	6.3		17.2	4.7	< 0.0001
Females	1986	length (mm)	46	67.2	6.8	40	61.8	9.1	< 0.0001
		weight (g)		30.1	9.4		23.6	11.9	< 0.0001
	1987	length (mm)	70	63.8	7.5	48	52.6	5.8	< 0.0001
		weight (g)		29.2	12.0		14.6	6.3	< 0.0001

RELATIONSHIP OF REPRODUCTIVE PARAMETERS WITH BODY SIZE

Fecundity, expressed as the number of mature oocytes per female, and reproductive investment, estimated by spawn mass, were both correlated with body size (fig. 2). The relationship between body size and fecundity may be described as an exponential model: for site A, N (oocytes) = $0.003L^{3.10}$ and for site B, N = $0.0018L^{3.19}$. The two models are not significantly different (covariance analysis after log-transformation. $F = 3.64$, df 1/47 [slope]; $F = 5.54$, df 1/48 [Y-intercept]). However, the coefficient of determination (r^2) shows higher variability at B (0.73 and 0.55 for 1986 and 1987, respectively) than at A (0.83 and 0.87). Such a relationship indicates considerable variation relative to size: while a 50 mm female laid 400 eggs, a 70 mm female laid 1600 eggs. Wet clutch mass was strongly correlated with female body size ($r^2 = 0.87$ and 0.90 for sites A and B, respectively). The relationship is also exponential: M (clutch mass) = $1.3 \times 10^{-5}L^{3.30}$ for site A and $M = 4.8 \times 10^{-7}L^{4.05}$ for site B. The difference between slopes, however, is not significant ($F = 3.69$, df 1/47). When the two populations are combined, the relationship becomes: $M = -14.9L^{4.18}$. The slope of the relationship between female length and average mass of a single egg (oocyte + capsule) was not strong. wet mass of a single egg = $-0.33L^{0.62}$, wet mass of the oocyte was related to female size ($r^2 = 0.65$) The linear model ($M = 0.13L^{-1.32}$) is acceptable for describing that last relationship (analysis of residuals) Dry mass was also related to female body size: $M = 0.02L^{-0.02}$ ($r^2 = 0.69$).

COMPARISON WITH OTHER EUROPEAN POPULATIONS

Table II presents fecundity and clutch mass for a 70 mm female in 13 European populations the adequate regression parameters of which were available in the literature. Table III shows different reproductive investments in 4 populations, estimated by the relationship of clutch mass to body mass Fecundity of frogs varies among populations with no apparent relationship to altitude, latitude or clutch mass. The 13 investigated populations are distributed among three groups: 5 populations had very low fecundity (fewer than 1300 eggs per 70 mm female), 6 had intermediate fecundity (1300 to 1600 eggs per female) and 2 had high fecundity (more than 1900 eggs per female) Populations from sites A and B in this study fall within the intermediate group. They are characterized by higher clutch masses and higher relative reproductive investments than are found elsewhere. Whether these parameters reflect a reaction to mortality induced by fishing or the consequence of a climatic cline (the studied populations represent those from South) is questionable. Data and measurements are needed from other populations, using comparable methods. Comparisons with other unfished populations in neighbouring areas might shed light on this problem. Figure 3 highlights the relationship between female length and dry egg weight in 6 populations Values are distributed linearly except for the population from Spitchwick (Devon, England), in which eggs were larger relative to female size when compared with all other populations.

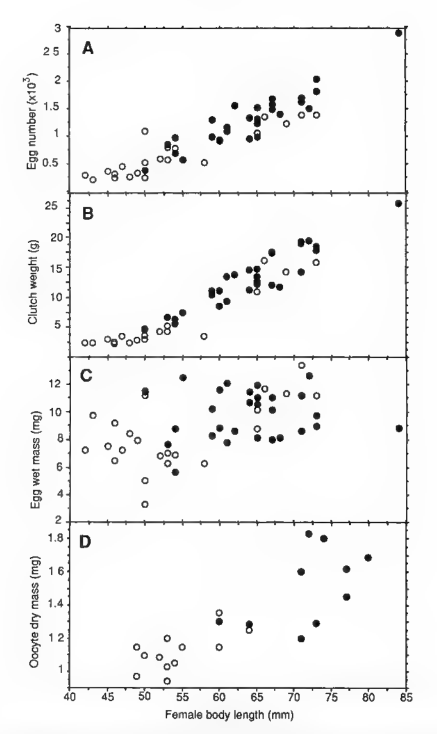


Fig. 2. - Relationship between female length and several demographic parameters. A: relationship with fecundity. B: relationship with clutch mass (clutch mass/n eggs). C: relationship with a single egg mass (before spawning). D: relationship with dry weight of an oocyte (each point is an average value for 30 oocytes). Black dots: site A (Servotte pond); open dots: site B (Thévenon pond).

Table II. - Fecundities of frogs from different European populations. Fecundity (N eggs) and clutch mass (weighed before spawning) were estimated for a 70 mm female using allometric models. Fecundity varies greatly from one site to another without clear relationship to altitude or latitude. Frogs under study show intermediate fecundity.

Region	Lat.	Alt (m)	N eggs	M clutch (g)	Authors
Berne (CH)	46°	600	~ 1000		RYSER, 1988 b
Haapavesi (FL)	64°10	100	1067	12.8	KOSKELA & PASANEN, 1975
Clare (IL)	53°		1140	12 8	GIBBONS & MCCARTHY, 1985
Tatras W (PL)	50°	1000	1199	11.5	KOZLOWSKA, 1971
Devon (GB)	50°31	100	1235		CUMMINS, 1986
Thévenon (F)	46°55	215	1383	14.3	This study
Lincolnshire (GB)	53°26	1	1533		CUMMINS, 1986
Beskid (PL)	50°	700	1538	14.5	KOZLOWSKA, 1971
High-Tatras (PL)	50°	1000	1538	12.1	KOZLOWSKA, 1971
Norfolk (GB)	52°42	60	1544		CUMMINS, 1986
Servotte (F)	46°58	200	1573	16.0	This study
Cracov (PL)	50°	200	1905	11.3	KOZLOWSKA, 1971
Cambridgeshire (GB)	52°26	10	1915		CUMMINS, 1986

Table III. - Comparison of reproductive investment of females from different populations. Frogs in the present study show a greater investment than populations from which data are available.

Region	Lat	Alt. (m)	M clutch/M body (%)	Authors
Poland	50°	1000	17.2	JUSZCZYK, 1959
North Finland	64°	100	20.3	KOSKELA & PASANEN, 1975
Thévenon 86	46°	210	39.38	This study
Thévenon 87	id.	id.	26 48	id.
Servotte 86	id.	id.	43.53	id.
Servotte 87	id.	id	38.25	id.

DISCUSSION

Average size of the common frog varies greatly among neighbouring demes and size variation is positively correlated to fecundity and egg size Why are frogs smaller in the "Bois de Champrougier"? Transfer among the studied ponds of eggs and tadpoles has occurred several times during the last twenty years, genetic homogeneity is probable.

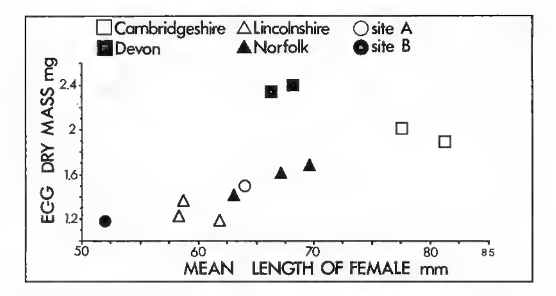


Fig. 3 - Relationship between means of female length and dry egg mass. Repetition of a symbol corresponds to data from several years. Data for English populations are from CUMMINS (1986); the population from Devon seems to show unusually large eggs.

Differences in size may be expressions of phenotypic plasticity influenced by subtle ecological variation. Any of three hypotheses may explain the smaller size of the Bois de Champrougier frogs:

(1) Small frogs experienced slower growth than large frogs.

(2) Small frogs are younger than large ones.

(3) Frogs are small when fishing is locally more intensive.

The first hypothesis assumes that maturity depends on age rather than on size or rate of growth. By contrast, the second hypothesis assumes that age at maturity depends on growth rate. Both hypotheses are theoretically acceptable (STEARNS & KOELLA, 1986). Age at maturity varies from one population to the other in the common frog, as well as within the same population. At low altitude, the common frog may mature in two or three years (GIBBONS & MCCARTHY, 1984), suggesting the major role of growth on maturation (RYSER, 1988 a). Variation of size from one year to the other may suggest the role of environmental constraints on either growth or recruitment (juvenile survival). The third hypothesis supposes that harvesting is, relatively to the population number, more intensive at Thévenon than at Servotte, leading the breeding population to be composed of a greater proportion of young animals. Such a hypothesis supposes that adult frogs reproduce more

than once. In Switzerland, at an altitude of 600 m, frogs seem to spawn twice during their life span (RYSER, 1986), but age structures observed at low elevation in Ireland (GIBBONS & MCCARTHY, 1984) and Spain (ESTEBAN RUIZ, 1990) indicate that adult mortality is so high that most females breed only once. All these hypotheses concern factors influencing maturation and longevity; determination of the age structure of each population becomes essential. The influence of harvesting will only be determined by comparing age structures of the present populations with populations which are not harvested in the same region.

In Europe, the relationship between size and fecundity shows great variation from one population to another and no clear correlation appears with altitude or latitude. Further description of local and annual variation within populations is needed prior to consideration of variation on a larger scale. The reproductive investment of Jurassian frogs seems higher than that observed in more Northern populations. SAVAGE (1961: 82) postulated (from data of BOULENGER and HÉRON-ROYER) that the higher fecundity of Southern frogs was an adaptation to higher tadpole mortality due to heat death. This hypothesis remains to be tested.

RÉSUMÉ

Des comparaisons de la taille corporelle de Grenouilles rousses entre des populations voisines en Bresse jurassienne (est de la France) montrent d'importantes variations. Les variations de taille sont corrélées à d'importantes variations de fécondité et de taille de l'œuf. Le nanisme est limité à des étangs qui sont tous situés dans le même massif forestier. Toutes les populations étudiées sont soumises à une pêche par des pisciculteurs professionnels, mais il n'est pas possible d'estimer l'impact de cette activité sur chaque population. La petite taille des Grenouilles pourrait résulter soit d'un ralentissement de croissance, soit d'un abaissement de l'âge d'acquisition de la maturité sexuelle, dû à la forte mortalité induite par la pêche. Les paramètres démographiques de ces populations françaises sont comparés à ceux d'autres populations européennes.

ACKNOWLEDGEMENTS

I am particularly indebted to MM MORESTIN and BOURDY, aquaculturists, for their collaboration in this work. I thank Dominique AUGERT, Stephen D. BUSACK, Louis CAILLÈRE, Alain DUBOIS, Günter GOLLMANN, Dominique PONTIER, Brian K. SULLIVAN and an anonymous referee for their criticisms on first drafts of the manuscript. The correction of the English version is due to Louis LEFEBVRE and Glyn THOIRON.

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Published with the support of
the Muséum national d'Histoire naturelle (Paris, France).

Directeur de la Publication: Alain DUBOIS.

Numéro de Commission Paritaire: 64851.

Alytes, 1991, **9** (3): 61-88.

Contents

Alytes is indexed in *Biosis, Cambridge Scientific Abstracts, Current Awareness in Biological Sciences, Pascal, Referativny Zhurnal* and *The Zoological Record.*

Imprimerie F. Paillart, Abbeville, France.
Dépôt légal: 3ème trimestre 1991.